

THE additions to the Zoological Society's Gardens during the past week include a Grant's Gazelle (*Gazella granti*) from East Africa, presented by Dr. Kirk; a Beccari's Cassowary (*Casuarinus beccarii*) from New Guinea, presented by Sir James Fergusson; an Owen's Apteryx (*Apteryx oweni*), two Weka Rails (*Ocydromus australis*), a Black Wood Hen (*Ocydromus fuscus*), from New Zealand, presented by Dr. G. Hector; two Australian Cranes (*Grus australasiana*) from Australia, presented by the Acclimatisation Society of Wellington, New Zealand; a Brown Indian Antelope (*Tetraceros subquadricornutus*) from India, a Dufresne's Amazon (*Chrysotis dufresniana*) from South-east Brazil, four Vulturine Guinea Fowls (*Numida vulturina*) from East Africa, an Anaconda (*Eunectes murinus*) from South America, purchased.

RECENT PROGRESS IN OUR KNOWLEDGE OF THE CILIATE INFUSORIA*

I BELIEVE that the object contemplated by the addresses which it has been the custom of your Presidents to deliver year after year to the Fellows of the Linnean Society will be best fulfilled by making them as much as possible the exponent of recent progress in biological science. The admirable addresses with which my distinguished predecessor has during his long tenure of office so greatly enriched our journal, afford an example as regards the exposition of botanical research which may well be followed in biology generally. The field, however, which thus offers itself is so wide, the activity in almost every department so intense, that the necessity of restricting the exposition within a limited area becomes imperative if it be expected to produce anything like a definite picture instead of a vast assemblage of images confused and ill-defined by their very multiplicity and by the condensation which would be inseparable from their treatment.

While thus imposing on myself these necessary limits, it is almost at random that I have chosen for this year's address some account of the progress which has recently been made in our knowledge of the CILIATE INFUSORIA—a group of organisms whose very low position in the animal kingdom in no way lessens their interest for the philosophic biologist, or their significance in relation to general morphological laws.

To enable you to form a correct estimate of the value of recent researches, it may be well to bring before you in the first place, as shortly as possible, the chief steps which have led up to the present stand-point of our knowledge of these organisms.

It is scarcely necessary to remind you that the first important advance which during the present century was made in our knowledge of the Infusoria dates from the publication of the great work of Ehrenberg,* whose unrivalled industry opened up a new field of research when, by his expressive figures and well-constructed diagnoses, he made us acquainted with the external forms of whole hosts of microscopic organisms of which we had been hitherto entirely ignorant, or which were known only by such figures and descriptions as the earlier observers with their very imperfect microscopes were able to give us.

Ehrenberg, however, as we all know, did not content himself with portraying the external forms of the microscopic organisms to whose study he had devoted himself, but sought also to determine their internal structure, of which scarcely anything had been hitherto known. In this direction, no less than in the other, the perseverance of the celebrated microscopist never flagged; but, unfortunately, at the very commencement of his researches he slid into a misleading path, and was never again able to find the right one.

Everyone knows how Ehrenberg, in accordance with preconceived notions of the high organisation of *all* animals, attributed to the Infusoria a complicated structure; how, while he rightly distinguished them from the Rotiferæ with which they had been confounded by previous observers, he yet regarded them as intimately related to these representatives of a totally different type; and how, in attributing to them a complete alimentary canal with numerous gastric offsets, he took this feature as their most important character, and designated them by the name of *Polygastrica*. And it is probably a matter of surprise to many of us, that with the overwhelming mass of evidence which subsequent research has brought to bear against the truth of the

polygastric theory, the great Prussian observer should still adhere with undiminished tenacity to his original views.

Among the authors who, since the publication of the "Infusionsthierehen" have contributed most to a correct estimate of the morphology, physiology, and systematic position of the Infusoria, the names of Von Siebold, Stein, Balbiani, Claparede, and Lachmann, and most recently, Haeckel, stand out conspicuously.

The first who from a strong position offered battle to the authority of Ehrenberg was Carl Theodor von Siebold.* Von Siebold rejected *in toto* the polygastric theory, and, so far from admitting a complexity in the organisation of the Infusoria, he regarded them as realising the conception of almost the very simplest form of life, and attributed to them the morphological value of a cell.

Let us see what is involved in this most significant comparison. The essential conception of a cell is, as you know, that of a more or less spherical mass of protoplasm with or without an external bounding membrane, and with an internal nucleus or differentiated and more or less condensed portion of the protoplasm. It was to a form of this kind that Siebold compared the body of an Infusorium. He called attention to the soft protoplasmic mass of which the body mainly consists; to the external firmer layer by which this is surrounded; and to the variously-shaped body differentiated in the protoplasm, to which Ehrenberg had gratuitously attributed the function of a male generative organ. Here then were, according to Siebold, the protoplasm body substance, the bounding membrane, and the nucleus of a true cell.

The morphological value thus attributed to the true Infusoria—under which were included the Flagellatæ—was extended by Siebold to Amœba and its allies, and to the whole assemblage so constituted he assigned the position of a primary group of the animal kingdom to which he gave the name of PROTOZOA, whose essential character was thus that of being unicellular animals. He then divided his Protozoa into those which had the faculty of emitting pseudopodial prolongations of their protoplasm (Amœba, &c.), and those in which the place of the pseudopodia was taken by vibratile cilia or by lash-like appendages. To the former he gave the name of *Rhizopoda*; to the latter he restricted that of *Infusoria*; and lastly he divided the Infusoria into the mouth-bearing, *Stomatoda* (Ciliata), and the mouthless, *Astomata* (Flagellata). From every point of view Von Siebold's conception of the morphology of the Protozoa, and his sketch of their classification, however much this may have been subsequently modified, must be regarded as marking out an epoch in the history of zoology.

Shortly after this the unicellular theory was strongly supported by Kölliker,† and received further confirmation from the researches of Stein,‡ who, however, was unable to accept it to its full extent. With an industry almost equal to that of Ehrenberg, Stein had the advantage of the more philosophic views of organisation which had emanated from the newer schools of biology, and to him we are indebted not only for more accurate views of the structure of the Infusoria, but for the first important contributions to our knowledge of their development; and though the opinion which he at one time entertained, that the true Acinetæ are only stages in the development of the higher Infusoria, has been abandoned by him, he has nevertheless demonstrated the presence in an early period of the development of certain species, of peculiar pseudopodial processes resembling the characteristic capitae appendages of the Acinetæ, an observation of importance in its bearing on the relations of these last to the true Infusoria. No doubt can remain, after Stein's observations, that the Infusoria in their young state have the morphological value of a simple cell, and it is only after their development has become advanced, and that a marked differentiation has begun to manifest itself in this primordial condition, that there can be any difficulty in accepting their absolute unicellularity.

About this time Balbiani drew attention to some very important phenomena in the life history of the Infusoria.§ It had been known even to the early observers that the Infusoria multiplied themselves by a process of spontaneous fission. They had been frequently observed in the act of transverse cleavage, and had also been noticed in what appeared to be a similar cleavage taking place in a longitudinal instead of a transverse direction. Balbiani, however, showed that this apparent longitudinal

* Siebold, "Lehrbuch der vergleichenden Anatomie," 1845.

† Zeitschr. f. Wissens. Zool., 1849.

‡ Stein, "Der Organismus der Infusionsthiere," 1867.

§ Balbiani, "Recherches sur les organes générateurs et la reproduction des Infusoires," *Comptes Rendus*, 1858, p. 383.

* Anniversary Address to the Linnean Society, by the President, Dr. G. J. Allman, F.R.S., May 24.

† "Die Infusionsthierehen als vollkommene Organismen." Leipzig, 1838.

cleavage had in many cases an entirely different significance; that it was, in fact, not the cleavage of a single individual, but the conjugation of two distinct ones; and he connected this phenomenon with what he regarded as a true sexual act.

It was then known that besides the nucleus which occupied a conspicuous position in the protoplasmic mass, there existed in many Infusoria another differentiated body similar to the nucleus but smaller, and either in close contact with it or separated from it by a greater or less interval. To this body the ill-chosen name of "nucleolus" had been given. Now, Balbiani's observations led him to believe that under the influence of conjugation this so-called nucleolus underwent a change and developed in its interior a multitude of exceedingly minute filaments or rod-like bodies, to which he attributed the significance of spermatozoa; while at the same time the nucleus became divided into globular masses, which Balbiani regarded as eggs, and in which he believed he could recognise a germinal vesicle and germinal spot. We should thus, according to this interpretation, have in the Infusoria the two essential elements of sexual differentiation, the spermatozoa and the egg.

Stein, though differing from Balbiani in certain details, accepts in its general facts the sexual theory, and maintains the spermatid nature of the rod-like corpuscles to which the nucleolus appears to give rise. But however real may be the phenomena described by Balbiani and by Stein, the correctness of assigning to them a sexual significance may be called in question; and it is certain that subsequent observation has not tended to confirm the hypothesis that we have in the Infusoria true eggs fecundated by true spermatozoa.

Claparede and Lachmann, two able and indefatigable observers fresh from the school of the great anatomist Johan Müller, now entered the field, and their joint labours have given us a great work on the Infusoria.* In this an entirely new view of the morphology of the Infusoria has been introduced. Receding widely from the unicellular theory of Siebold, they approximate towards the views of Ehrenberg in assigning to the Infusoria a comparatively complex structure; but instead of adopting the polygastric theory of the Prussian microscopist, they attribute to the Infusoria a single well-defined gastric cavity occupying the whole of the space limited externally by the outer firm boundary walls of the softer protoplasmic mass; while this mass is regarded by them as nothing more than a sort of chyme by which the gastric cavity is filled. According to this view, the nearest relations of the Infusoria would be found among the zoophytes, and their proper systematic seat would be in the primary group of the Coelenterata.

Though few zoologists will now be prepared to accept the conclusions of the Genevan naturalists, the coelenterate relations of the Infusoria has recently found an advocate in Greeff.† In an elaborate memoir on the Vorticellæ, Greeff sees in the very well-marked distinction between the external or cortical layer and the internal soft body-substance, a proof of the views maintained by Claparede and Lachmann; and he considers this position still further confirmed by the presence in *Epistylis flavicans* of numerous oval or piriform, brilliant, well-defined capsules, which are generally distributed in pairs below the outer layer, and which, under the influence of a stimulus, emit a long filament, thus closely resembling the thread-cells so well known as characteristic elements in certain tissues of the Coelenterata.

It must be here remarked that the presence of similar bodies in the Infusoria, where they have been described under the name of trichocysts, has long been known. Though varying in form, they all possess a more or less close resemblance to the thread-cells of the Coelenterata. Their presence undoubtedly indicates a step upwards in the differentiation of the organism, but, as we shall presently see, it offers no valid argument against its unicellularity.

In his admirable "Principles of Comparative Anatomy,"‡ Gegenbaur expresses doubts as to the sexual nature of the reproductive phenomena of the Infusoria, and is disposed to regard the so-called embryo-sphere, to which the nucleus gives rise, in the light of a proliferous stolon, from which several zooids are in some cases thrown off. Arguing from the Acinetæ-like form of the young in the higher Infusoria, as shown by Stein, and comparing the transitory condition of this with the permanent condition of the true Acinetæ, he

believes that we are justified in regarding the Acinetæ as the ancestral form from which the proper Infusoria have been derived. He further compares the contractile vesicle and its canals in the Infusoria with the water vascular system of the worms, and believes that a parentage with these higher forms is thus indicated. Gegenbaur, moreover, expresses himself strongly against the unicellular theory. He regards, however, the absence of distinct cell nuclei in the substance of the Infusoria as affording evidence of their composition out of several "Cytodes" or non-nucleated protoplasm masses rather than out of true nucleated cells.

Still more recently Bütschli has given us the results of observations on the conjugation of *Paramecium aurelia*.* He is led, however, to doubt the validity of the sexual interpretation of the conjugation. He found that in certain cases in *Paramecium aurelia* and in *P. colopoda* the so-called spermatid capsule into which the nucleolus had become converted, had entirely disappeared without any evident change in the nucleus; and he concludes that fecundation of the bodies regarded by Balbiani as eggs cannot be here entertained. Indeed, he will not allow that we have evidence entitling us to regard the appearance of filaments in the interior of the nucleolus as affording any indication of true spermatozoa. He offers no explanation of this appearance, but he calls attention to the fact that both Balbiani and Stein noticed that in *transverse* division of the Infusoria—a phenomenon with which conjugation can have nothing to do—the nucleolus frequently enlarges and acquires a longitudinal striation like that of the nucleolus in the supposed production of spermatozoa during conjugation. Balbiani maintains that this striation during cleavage is only superficial, but it nevertheless affords an argument against assigning any more important significance to the very similar appearance in the case of conjugation.

On the whole it would appear that the spermatid nature of the striæ visible in the nucleolus of the conjugating individuals—even admitting that these striæ represent isolatable filaments—has not by any means been proved, while the phenomenon of conjugation in the Infusoria would seem to correspond rather with the conjugation so well known in many lower organisms, where it takes place without being in any way connected with the formation of true sexual products.

In the same memoir the results of observations on some other points in the structure and economy of the Infusoria have also been given by Bütschli. He records the occurrence of minute crystal-like laminae in the interior of a marine Infusorium (*Strombidium sulcatum*) rendered remarkable by a conspicuous girdle of trichocysts which surround its body. The crystal-like corpuscles seem to be of the nature of starch, for on the application of iodine they assume a beautiful violet colour. It does not appear from Bütschli's account of these bodies that they have not been introduced from without, and the chief interest of the observation seems to be in the discovery of an amylaceous body assuming a crystalline form. He had previously met with similar bodies in a parasitic Infusorium (*Nyctotherus ovalis*), as well as in a Gregarina (*G. blattarum*).

He also describes, under the name of *Polykricos Swartzii*, a new Infusorium which he frequently found in the fjords of the south coast of Norway and in the Gulf of Kiel, and which he regards as especially interesting, from the fact that with a true infusorial organisation it contains, irregularly distributed in the outer layer of the body, numerous capsules indistinguishable from the true coelenterate thread cells. These bodies, however, are never included in a special investment, and he justly regards their presence as affording no argument against the unicellular nature of the Infusoria. He lays it down as a probable distinction between the trichocysts of the Infusoria and genuine thread-cells, that the former have the power of ejecting their contained filament from both ends of the capsule, while we know that in the thread cell it is only one end which gives exit to it. This double emission of a filament appears to have been observed by Bütschli in the trichocysts of a large Nassella, but the distinction is certainly not a generally valid one. There is no doubt that in the majority of cases the trichocyst emits its filament from only one end of its capsule, exactly as in the thread cells of the Coelenterata, and it is hard to see in what respect the bodies noticed by Bütschli in his *Polykricos Swartzii* essentially differ from true infusorial trichocysts. In conclusion, he declares himself strongly in favour of the unicellularity of the Infusoria.

(To be continued.)

* Claparede et Lachmann, "Études sur les Infusoires et les Rhizopodes." Genève, 1858-61.

† Greeff, "Untersuchungen über den Ban und die Naturgeschichte der Vorticellen." Archiv für Naturg., 1870.

‡ "Grundsätze der Vergleichenden Anatomie," 1870.

* O. Bütschli, "Einiges über Infusorien." Archiv f. Microscop. Anat., 1873.